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COMMENT ON A RATE TEST

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Turelli et al. (1988) proposed a "rate test" regarding whether the speed of evolution is too fast or too slow to be explained by drift under certain assumptions. Their test involves the count t of generations of a lineage, the absolute change z in the mean of a phenotypic trait over that span of generations, and the new genetic variance σ_m^2 introduced by mutation per zygote per generation. Evolution has been too fast to be explained by drift if

$$\sigma_m^2 < \frac{z^2}{2t(2.2414)^2}$$

and has been too slow to be explained by drift if

$$\sigma_m^2 > \frac{z^2}{2t(0.03134)^2}$$

(Turelli et al., 1988 eqs. 9 and 10). I have cancelled a factor σ^2 from both sides and substituted more accurate normal tails for the values 2.24 and 0.03 used by Turelli et al. Together the formulas delimit one possible 95% confidence interval around the null hypothesis of drift. This particular interval covers a range of z's in the ratio of 2.2414 : 0.03134, which is 71.5 to 1.

When phenotypic means are available at an adequate number of intermediate times, a far more powerful statistical test for the "slow" side of this same distinc-

tion is available from the theory of random walk. Instead of the measure z of absolute change from end to end of the series, one should use the maximum excursion z^*, the largest (absolute) deviation from the starting sample mean *anywhere* in the series of t generational means. Then, under the assumptions of the "mutation-drift-equilibrium" model, as summarized in Turelli et al. (1988 eq. 6), evolution is too fast to be explained by drift if

$$\sigma_m^2 < \frac{(z^*)^2}{2t(2.4977)^2}$$

and is too slow to be explained by drift if

$$\sigma_m^2 > \frac{(z^*)^2}{2t(0.56014)^2}.$$

The range of the implied 95% confidence interval for drift, again on the multiplicative scale, is 2.4977: 0.56014, which is 4.46 to 1, a 16-fold improvement over the bound supplied by Turelli et al.

These bounds on the ratio z^*/σ_m are a consequence of a fundamental theorem about Brownian motion proved by Erdös and Kac in 1946 but suspected by the economist Bachelier around the turn of the century (see Spitzer, 1964). The theorem is stated and one proof

sketched in Bookstein (1987); a 90% confidence interval is shown and a multivariate extension presented in Bookstein (1988).

In practice, the biologist is unlikely to have observed a series of phenotypic means at every single generation over any period longer than one human life. Instead, long series typically take the form of $k + 1$ subaggregated means $S_{t_0} \ldots S_{t_k}$ corresponding to noncontiguous strata spanning a total time $t = t_k - t_0$. On the null model of random walk, a reasonable estimate of $2t\sigma_m^2$ is just $\sum_{i=1}^{k}(S_{t_i} - S_{t_{i-1}})^2$. Actually, this is estimating $t\sigma^2$, the net variance of the process over t generations, under the assumption of independent increments of variance σ^2 between each consecutive pair of generations. In this form, it incorporates the effects of any nongenetic determinants themselves following random walks, unless these are systematically partialled out by reference to explicit proxy measures. In this estimate, small fluctuations in effective population size are taken into account, even away from equilibrium, by the averaging over intersample epochs i. (The possibility of a discrete bottleneck of much higher evolutionary speed may be examined by the method of Bookstein [1987].) The approximate distribution of the statistic $(z^*)^2/t\sigma^2$ based on this estimate seems reasonable for k greater than 10 or so whenever the distribution of differences between successive subsample means is not too longtailed. Bookstein (1988) uses this statistic in a reanalysis of Bell et al.'s (1985) stickleback data, means for six characters in 26 strata spread over some 100,000 years of evolution.

The lower bound for σ_m^2 on the neutral model is, in a sense, equivalent in the two approaches. The value 2.2414 is the 0.0125 normal tail, 2.4977 is the 0.00625 normal tail, and the upper tail-probabilities for the maximum excursion z^* are almost exactly twice those of the corresponding tail-probabilities for a conventional normal deviate (see Bookstein, 1987). But different histories may be flagged as "too fast" by the two tests. When drift is rejected by the z^* test, the alternate hypothesis of "too fast" includes various patterns of change that would perhaps not be called "trends," such as a U-shaped history which heads away from its starting value and then reverts.

By substituting the maximum excursion z^* for the final excursion z, the constant in the upper bound for σ_m^2 on the neutral model is sharpened from 0.03134 to 0.56014. This is because, under the null model of drift, the probability of having left a narrow band of values around the starting state is high even when one knows that there has been a reversion to that starting value at some later time. The greater power of the test for stasis using z^* derives from the exploitation of the assumption that drift describes the values of all the observations of the time-series, not just the last, in relation to the starting value. When such intermediate data are available, the maximum-excursion test is generally to be preferred. For instance, an evolutionary history that travels $5\sigma_m\sqrt{t}$ from its starting value and then returns all the way to that starting mean would be called "too slow for drift" by the z test, but "too fast for drift" by the z^* test, a considerable difference indeed.

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